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Water Deficit Condition Affecting Rice Production – Challenges and Prospects

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1. Introduction

Drought is one of the inherent abiotic constraints that affect agricultural productivity worldwide. It is estimated that drought stress can potentially reduce nearly 20% of crop yield around the World (Bouman et al., 2005; Scheiermeier, 2008). Global climatic changes such as dry spell, heat waves and uneven precipitation patterns limit water availability for farming (Bates et al., 2008). However, water is needed at every phase of plant growth from seed germination to plant maturation (Athar & Ashraf, 2005; Chaves et al., 2003) and any degree of imbalance in the uptake would pose a serious threat to agriculture by adversely affecting the growth and grain yield (Wang et al., 2001). Further, water deficit stress could occur at any time of growing seasons; however severity of stress effect on productivity depends on distribution of rainfall.

Rice is the staple food for almost half of the world population. Rice farming is considered as one of the world's most sustainable and productive cropping system, as it is adapted to wide range of environment ranging from tropical low lands to mountains and from deep water swamp to uplands. In general, rice crop is semi aquatic and can thrive well in waterlogged soil and hence its production system relies on ample water supply. Based on the availability of water, rice can be grown in different ecological conditions such as low land rainfed, low land irrigated, deep water and upland. In global scenario, irrigated rice is considered as productive farming system and has accounted for 55% of total harvested area with a contribution of 75% of total productivity. Further, annual productivity of irrigated rice is estimated to be 5% more than that of rainfed rice (Fairhurt & Dobermann, 2002). Meanwhile, resource for irrigation has declined gradually over the past decades due to rapid urbanization and industrialization which exacerbates the problem of water scarcity (Gleick et al., 2002). Current rice production systems rely on ample supply of water and it is estimated that on average rice require 1900 liters of water to produce 1kg of grain. Even a short period of water deficit is highly sensitive to rice farming and rice productivity (O'Toole, 2004). Different developmental stages of rice such as tillering phase, panicle initiation and heading known to respond differently to drought stress (Botwright Acuna et al., 2008; Kamoshita et al., 2004), however, factors such as timing, intensity and duration of stress have detrimental effect on plant growth. Liu et al., (2006) reported that reproductive stage, especially during flowering, is more vulnerable to stress and cause spikelet sterility.

Rice-cropping system is considered as economic backbone of many Asians as 90% of the World total rice is grown and consumed in Asia. A small decrease in availability of water would drastically affect grain yield and imperil food security. Increasing crop tolerance to water scarcity would be the most economic approach to improve the productivity and to minimize agricultural use of fresh water resource. To fulfill this objective, a deeper understanding of the possible mechanisms under water stress environment is a must. Recent studies have shown that plants have evolved various morphological, physiological, biochemical and molecular mechanisms to cope up with adverse climatic effect. Conventional breeding strategies utilized those mechanisms to certain extent and achieved a linear improvement in yield by exploiting genetic variation of phenotypic traits in the germplasm (Atlin et al., 2006; Lafitte et al., 2006; Serraj, 2005). However, development of tolerant varieties to water deficit condition has been slow due to lack of understanding on the mechanism of drought tolerance. Several efforts have been made to improve crop productivity under water limiting environment. Munns (1993) suggested that physiological based approach could furnish a new insight to breeding programme by offering reliable key indicators for screening drought tolerant genotypes to improve crop yield over a range of environment. Nevertheless, very little information is available on magnitude of genetic variation associated with physiology of tolerance. Furthermore, plants evolve a wide spectrum of adaptive mechanisms from whole plant to molecular level which varies within species and cultivars to overcome drought stress (Bartels & Sunkar, 2005; Jones, 2004; Rampino et al., 2006; Yamaguchi Shinozaki and Shinozaki, 2005). To exploit genetic basis of physiological variations effectively, investigations on molecular basis of stress are indispensable. Rapid advancement in molecular techniques helps to elucidate the control mechanisms linked to stress perception and responses by dissecting yield and integrative traits influenced under stress. Number of drought inducible gene and gene products have been identified at transcriptional and translational level and most of the gene products may function in stress tolerance at cellular level (Umezawa et al., 2006; Yamaguchi Shinozaki & Shinozaki, 2005; Zang et al., 2004). Further, all these investigations have provided important clues for functional characterization of stress responsive gene and stress tolerance mechanism; thereby widen our knowledge in mitigation of drought stress. The present review addresses the recent advances of the adaptive strategies in rice and facilitates the development of enhanced tolerance by integrating functional genomics into breeding programs.

2. Physio morphological traits for yield under drought stress

In rice, a number of physio-morphological putative traits have been suggested to confer drought tolerance (Deivanai, et al., 2010). Indeed, root system architecture plays a primary constitutive role in acquisition of water and nutrient from the soil and maintains plant water status (Nguyen et al., 1997; Lafitte et al., 2001; Kato et al., 2006). Descriptors of root architecture such as rooting depth (Pantuwan et al., 1996; Wade et al., 1996), root density, root thickness, root distribution pattern (Lilley and Fukai, 1994; Fukai and Cooper, 1994) increases plant water uptake and avoid dehydration mechanism. However, water uptake efficiency is determined by the function of root length, soil type, root hydraulic conductance and transpiration demand (Nobel, 2005). Further, root system architecture is highly dynamic and its functions are affected by change in environmental conditions and soil types (Lafitte et al., 2001). Since root characteristics are invisible for direct selection, knowledge on

interrelationship between plant type and root architecture would be desirable to facilitate yield performance of rice varieties under different water regimes.

Traditional plant breeding has identified traits such as plant type (plant height, tiller number, leaf area, leaf area index), phenology (timing of germination, floral initiation, flowering and seed maturity) and canopy temperature for screening of genotypes to improve grain yield under stress (Turner, 1982; Cooper et al., 1999; Slafer, 2003; Turner, 2004; Reynold et al., 2005a). In fact, grain yield is a complex quantitative trait attributed by number of panicle/shoot/m², grains/spikelet/panicle and grain weight / panicle (Sinha and Kanna, 1975). Improvement of crop yield could be achieved by selecting the genotypes based on the intensity of genetic variation. Several investigations have observed significant genetic variation for root number, diameter, depth, branching, root to shoot ratio, water extraction and root penetration (Yadav et al., 1997; Lafitte et al., 2001; Price et al., 2002b; Pantuwan et al., 2002a & b; Nhan et al., 2006). Meanwhile, high heritability was also noticed for root thickness, root dry weight and root length density (Lafitte et al., 2001). Moderate heritability for grain yield was reported by Babu et al., 2003; Atlin et al., 2004; Lafitte et al., 2004b; Yue et al., 2005; Kumar et al., 2007. Though, several traits were considered for improving drought tolerance in rice, only few have contributed significantly towards grain yield under drought condition (Lafitte, 2003). It is because most of the traits that respond to stress are constitutive and are not adaptive to stress (Parry et al., 2005; Komoshita et al., 2008). Further, substantial differences in root system architecture and grain yield have been reported between species, cultivars and land races. Obviously, grain yield is characterized by yield potential of the genotypes under target environment and intrinsically linked with plant water status (Araus et al., 2003; Rizza et al., 2004; Blum, 2005), a relevant physiological measure of interest under drought prone environment. Plant water status is determined by a balance between water uptake through root system and demand by shoot. Since plant production is the function of water use (WU), water use efficiency (WUE) and harvest index (HI), it is therefore vital to understand its effect during defined developmental stage to design effective selection method to improve plant production under dry environment. Several direct measurements are recommended to assess plant water status and its physiological consequences, some widely used measures are mentioned in this review

2.1 Water use efficiency (WUE)

WUE provide the means of efficient use of water and serves as a breeding target in water saving agriculture. Traditionally defined as the ratio of dry matter produced per unit of water transpired, and constitute one of the key determinants in controlling plant production. It is also referred as “transpiration efficiency” and estimated from the measures of leaf gas exchange or by using carbon isotope discrimination. Mean while, carbon isotope discriminant method had contributed much in the study of WUE and provided large volume of data in relation to genetic diversity and plant breeding. Studies have shown that yield related traits such as biomass accumulation and transpiration rate are highly interlinked with stomatal control and leaf area (Cabuslay et al., 2002; Richards, 2000; Tardieu & Tuberosa, 2010). For example, when plant experienced mild water stress, it increased WUE by regulating stomatal conductivity and lower carbon isotope discriminant measures. In most of the drought related studies low measures of carbon isotope discrimination found to be associated with high WUE. Higher WUE in turn lower photosynthetic rate due to reduced rate of transpiration and consequently slower the rate of

plant growth (Codon et al., 2004). It is obvious that increased WUE has resulted in smaller or short duration plants with reduced transpiration, biomass production and yield potential due to reduced water use. Blum (2005) pointed out that high WUE is largely a function of reduced WU and suggested that it can be used as a yardstick to measure irrigation efficiency in agriculture. Further, he proposed direct selection of plant type with moderate growth, short duration and reduce leaf area would promote WUE. Currently, agricultural sectors are slowly progressing due to use of genotypes with increased WUE and improved agronomic practices (Pereira et al., 2006; Richards et al., 2002).

2.2 Leaf water potential (LWP)

Leaf water potential (LWP), a measure of whole plant water status and has long been recognized as an indicator for dehydration avoidance (Pantuwan et al., 2002). When water deficit in leaf goes beyond a threshold level, stomata closes as a response to lower the rate of transpiration. According to Hsiao and Bradford (1982), stomata functions as safety valve to regulate water loss when tissue water status becomes too low, whereby minimize the severity of water deficiency in plants. Thus higher LWP is maintained by stomatal closure and varietal differences in stomatal response to water status have been reported by Jongdee et al., (1998), O'Toole & Cruz (1980) and Turner (1974), it is mainly due to differential capacity of hydraulic conductance among the genotypes. Further, genotype with deeper and thicker roots shown to extract more soil moisture effectively and maintains higher plant water status (Yoshida & Hasegawa, 1982). In a study, Sibounheuang et al., (2001) observed consistence in the performance of LWP and suggested a mighty relation between shoot water potential and internal plant water conductivity. Mean while, Kumar et al., (2004) reported a positive association between grain yield and relative water content with LWP.

Stomatal closure found to increase leaf temperature and measure of canopy temperature serves as an indirect measure of plant water status. Boonjung and Fukai (1996) as well as Pantuwan (2000) observed taller genotypes tend to have larger canopy than the shorter genotypes and they found smaller canopies had lower demand for water and were able to maintain higher LWP. The two parameters namely leaf rolling and leaf death are considered as determinant for estimating LWP. Earlier studies have reported higher estimates of visual scores and heritability for those two determinants while screening cultivars for drought tolerance.

2.3 Osmoregulation

Osmoregulation is receiving increasing recognition as an effective physiological mechanism of drought tolerance. Drought stress known to alter internal plant water status and lower water potential of cell environment (Babu et al., 1999). As a consequence, solutes are actively accumulated at high concentration within cells in order to maintain water potential (Blum, 1998; Kramer & Boyer, 1995). Such solutes are referred as osmolytes which include amino acids, sugars, polyols, quaternary ammonium and sulfoium compounds (Rontein et al., 2002). According to Blum (1998) the process of accumulation of solutes during the development of water shortage and enabling the plant to maintain hydrated state is termed as osmotic adjustment (OA), while buffering mechanism against dehydrated condition by addition or removal of solutes from cytoplasm is osmoregulation.

Generally, OA restores turgor pressure of both root and shoot, thereby permit stomatal conductivity to continue and help to sustain plant growth at time of transpirational demand

(Blum, 1996, 2005; Serraj & Sinclair, 2002; Stoop et al., 1996). Further, Blum (1996) found that these compounds stabilize macromolecular structures and membrane proteins. Nevertheless, the role of osmolytes are diverse and investigations on osmoprotectants have revealed that proline regulates cellular redox during stress (Kuznetsov & Shevyakova, 1999) while, mannitol protects oxidation sensitive cellular structure by scavenging reactive oxygen species (Huang et al., 2000) whereas, trehalose and fructan function as membrane stability (Nakayama et al., 2000), aquaporin, a major intrinsic protein super family facilitate control of water permeability through membrane (Luu & Maurel, 2005).

A genetic variation of 0.3 – 0.5 MPa has been reported for OA in rice (Turner et al., 1986). Though OA enable to maintain water absorption and cellular turgor pressure, a number of contrasting reports have been published. For instance, Munns (1988) pointed that OA may not show positive effect on plant growth and grain yield. It was also argued that OA occurs in root facilitates elongation of root growth at the onset of soil drying and in turn assist the root to penetrate deeper in search of resources thereby enable the plant to extract more soil water. Serraj & Sinclair (2002) found that plants with higher root penetration capacity is capable of sustaining plant growth and they suggested investigation on OA with focus on roots and root tips would elucidate the role of OA in practical breeding.

2.4 Stay green

Retention of greenness in leaves helps the plants to live longer and increase crop productivity; hence this trait is considered as one of the key determinants for developing drought resistance in rice (Fukai & Cooper, 1995). Genotype possessing stay green trait maintain high photosynthetic activity often protects the plants from premature senescence (Campos et al., 2004) during the onset of stress. It is reported that stay green plants assimilate more nitrogen and retain high level of nitrogen content in the leaf, thereby retains photosynthetic capacity under water limited conditions (Borrell et al., 2001). Further it enhances the transpiration efficiency and enable the plants to use more water to ensure continuous availability of new assimilate thereby increase the grain filling and size. Studies have also shown that stay-green is positively associated with grain yield

3. Functional genomic approach

In the past decades, integration of physiological and biochemical studies on abiotic stresses have contributed extensively in identifying tolerance traits responsive to stresses (Richard, 2000). Conventional breeding techniques attempted to utilize genetic variations of those traits from varietal germplasm; however the success is limited by: i) complexity of stress responses, ii) low genetic variation of yield component under stress condition and iii) lack of suitable selection technique (Ashraf, 2010; Cushman & Bohnert, 2000). Recently engineering of drought tolerance in plants is being pursued as viable option as it seems to be more attractive and rapid approach for breeding drought tolerance. Since transfer of functional genes that are directly involved in drought mechanism by genetic engineering is complex, the success of present engineering strategies rely on understanding of key gene network and regulatory control of biological processes associated with drought stress (Seki, et al., 2003; Shinozaki et al., 2003). Further, the advent of high throughput genomic platforms has facilitated increasing number of tools and resources for elucidation of abiotic stress responses in plants. Furthermore, large scale genome sequencing projects has generated a

number of sequence information from DNA microarrays, serial analysis of gene expression (SAGE), cDNA fragment sizing combined with amplified fragment length polymorphism (cDNA – AFLP), differential screening of cDNA libraries, expressed sequence tag (EST) sequencing, massive parallel signature sequencing (MPSS) etc., provides important clues for gene expression, functional characterization and identification of stress responsive genes (Bohnert et al., 2006, Parray et al., 2005; Umezawa et al., 2006).

More recently several stress inducible novel putative genes have been identified from wide range of tissue specific for genetic engineering. Meanwhile, sequencing project also enabled the development of molecular markers such as RFLPs, RAPDs, CAPS, PCR indels, AFLP, microsatellite such as SSR and SNP that are closely linked to target loci and facilitated mapping of quantitative traits loci (QTLs) for agronomically important attributes under drought stress (Lafitte et al., 2004; Talame et al., 2004). Subsequently those markers were used for marker assisted selection (MAS), a powerful tool for indirect selection of complex traits at early stage. However the efficiency of MAS depends on the distance between observed QTL and marker loci and also the magnitude of additive variance explained by QTL (Blumwald, et al., 2004). Thus the key role of functional genomics is to deduce the biological function of gene and gene products through genomic approaches like genetic mapping, transcriptional profiling and proteomics.

3.1 Quantitative trait loci (QTL) to dissect drought stress related traits

Progress in genomic sequencing of rice has facilitated a range of approaches to identify molecular markers (Nguyen et al., 1997), which examines the inheritance pattern of QTL in response to drought stress. Further these markers explore chromosome regions controlling genetic variations of physiological traits and play a central role in construction of linkage map using QTL analysis. QTL mapping approach has successfully identified a number of genetic regions that are expected to be associated with drought response, such as plant height and flowering time (Ishimaru et al., 2004; Li et al., 2003), root architecture (Courtois et al., 2003; Kamoshita et al., 2002; Price et al., 2002c; Tuberosa et al., 2003; Venuprasad et al., 2002; Zheng et al., 2003), root penetration (Johnson et al., 2000; Nguyen et al., 2004; Zheng et al., 2000), stay green phenotype (Jiang et al., 2004). OA, RWC and leaf rolling (Robin et al., 2003; Zhang et al., 2001), LWP (Yan Ying et al., 2008), leaf drying (Lafitte et al., 2004), yield and yield component under drought stress (Babu et al., 2003; Bernier et al., 2008; Campos et al., 2004; Kamoshita et al., 2008; Kumar et al., 2007; Lafitte et al., 2004; Lanceras et al., 2004). Most of the mapping populations were derived from cross between upland japonica and low land indica cultivars (Courtois et al., 2003) under varying water regimes, further these studies identified the location of drought tolerant traits as well yield and yield components under stress on chromosomal regions. For example, Babu et al., (2003) documented the location of drought tolerant QTLs in rice in the regions of chromosome 1 (plant water status), chromosome 3 (biomass yield under stress), chromosome 4 (root morphological traits) and chromosome 9 (RWC and delayed flowering due to stress). Whereas another group (Lanceras et al., 2004) mapped physio-morphological traits and confirmed the region of QTL traits in chromosome 3 (Grain yield, biomass and delayed flowering), chromosome 4 (grain yield) and chromosome 8 (biomass yield and spikelet sterility). In both the studies, the traits such as biomass, yield and yield components were found to be common and located at the same intervals on chromosome 3, 4 and 9. In another study, Bernier et al., (2007) while evaluating F₃ progenies derived from a cross between two upland rice cultivars

under field trials for two years, identified a stable QTL for drought tolerance on chromosome 12 linked to grain yield, biomass production, harvest index, plant height and early flowering. Wealth of information thus generated on QTL over last two decades helps to develop strategies for marker assisted selection (MAS) to screen drought tolerant strains at early stage of growth. Several studies have been conducted under both well watered and drought stressed conditions and a significant progress has been made during last few years in marker assisted selection (Jearakongman, 2005; Price et al., 2002c; Shen et al., 2001; Yue et al., 2005; Steel et al., 2006). One of the classic achievement of MAS is the release of first ever highly drought tolerant Indian rice variety “Birsa Vikas Dhan III (PY,84)”, characterized by early maturity, good quality high grain yield (Steele, 2009). Though several putative loci for drought stress tolerance have been identified, the contribution of MAS to development of drought stress tolerant cultivars has been marginal. The effectiveness of MAS is challenged by number of factors such as: i) accuracy and preciseness of phenotyping of traits, ii) very large genetic x environment interaction component wherein the QTL established in one environment often disappear in another and iii) poorly defined genetic architecture of polygene controlling yield (Ashraf, 2010; Cattivelli et al., 2008).

The efficiency of MAS could be improved through map based cloning (MBC), where specific QTL is introgressed into sensitive cultivars through pyramiding, a process of combining several genes together into single genotype (Steele et al., 2006). To date most plant QTLs have been cloned by positional cloning approach using functional markers with a goal to identify candidate gene responsible for drought stress and to manipulate the target trait more directly. Most of the comprehensive physical map reported from the earlier studies covers a region of 35-64 cM resolution which may contain several hundred to few thousand genes, need to be fine mapped. High density genetic map using single nucleotide polymorphism (SNP) and other marker may precisely detect QTL genes associated with drought tolerance. Further, fine mapping of specific QTL regions could be achieved by developing near isogenic lines (Nguyen et al., 2004). However, identification and characterization of QTL genes involved in regulatory network is still remain challenging.

3.2 Transcript profiling

ESTs provide a direct approach for discovering genes in response to stress, with the advent of high throughput transcriptome studies, several ESTs have been generated from different cDNA libraries (viz., full length, normalized and subtracted) which offered a foundation in deciphering the role of regulatory network in stressed tissues derived at various developmental stages (Goff, 1999). Numerous putative genes respond to dehydration stress have been categorized by EST based gene expression profiling (Shinozaki et al., 2000; Yamaguchi - Shinozaki & Shinozaki, 2006). Some of these genes that are induced during stress protects the plant cell directly while the others involved in signaling cascades with diverse pathways, suggesting the complexity of the mechanism involved in sensing and responding to multifarious stresses (Bartels & Sunkar, 2005; Blumwald et al., 2004; Bray et al., 2000). Further, the plasticity of plant response to water limited conditions is governed by a number of transcription factors (TFs) which can modulates and regulates various stress inducible genes either independently or constitutively. More than 50 different TFs have been identified and characterized, are found to be member of large multigene families such as bZIP- (Martinez-Garcia et al., 1998), MYB (Jin & Martin, 1999), MYC, AP2/ERF (Riechmann,

& Meyerowitz., 1998) , NAC (Kikuchi et al., 2000) and WRKY (Dong et al., 2003). Many genes that respond to multiple stresses are induced by abscisic acid (ABA); a phytohormone which acts as a key signaling intermediate in controlling the expression of stress related genes. A detail examination of ABA regulated genes has shown the presence of both ABA dependent / independent regulatory systems in ABA biosynthesis (Vinocur & Altman, 2005; Yamaguchi-Shinozaki & Shinozaki, 2005). Further, the transcriptional factors such as MYC and MYB function as activator in one of the ABA-dependent regulatory system, while a cis-acting element known as drought responsive element factor/ C-repeat (DREB/CRT) is involved in ABA-independent regulatory system (Shinozaki et al., 2000). Several experimental approaches on genomic analysis have reported different TFs that are associated with stress responsive gene induction are presented in Table 1.

TF family	Gene category	Gene name	Physiological response	Reference
AP2/ERF	DREB1/CBF	OstDREB1A	Stomatal closure	Ito et al., 2006; Oh et al., 2005; Xiao et al., 2009
NAC	SNAC	AtSNAC1	Stomatal closure	Rabbani et al., 2003
bZIP	AREB/ABF	AtABF3	Reduced leaf rolling and wilting	Oh et al., 2005
TFIII-A Zinc finger	ZFP252	OsZFP252	Proline and sugar accumulation	Xu et al., 2008
NF-Y (A, B, C)	NF-YB	AtNF-YB1 ZmNF-YB2	High photosynthesis	Nelson et al.,2007
WRKY Zinc finger	WRKY	OsWRKY11	Reduced leaf wilting and slow water loss	Wu et al., 2009
EAR Zinc finger	Zat10/STZ	AtZat10	High spikelet fertility and grain yield	Xiao et al., 2009

Table 1. Genome wide transcriptome analysis of drought response in rice

To date, substantial amount of published works have examined the mechanism of plant response to various environmental changes and demonstrated that some transcription factors significantly overlaps with the expression of gene that are induced in response to different stress (Chen & Murata, 2008; Seki et al., 2001). Further, overexpression of one or more transcription factors confirmed the activation of TF regulons that modulate a wide range of signaling pathways in achieving tolerance under multiple stress conditions (Umezawa et al., 2006). For example, it enables the regulation of key enzymes in the biosynthesis of compatible solutes such as proline (Ito *et al.*, 2006; Zhu et al., 1998), glycinebetaine (Quan et al., 2004), variety of sugars and sugar alcohol, viz., trehalose (Garg et al., 2002), manitol (Abebe et al., 2003), galactinol and raffinose. Transgenic rice plants produced by overexpression of transcription factors help to understand and manipulate the

responses of plant stress. Considerable progress has been made in developing transgenic rice strains that are tolerant to drought stress and the results are summarized in Table 2.

Gene	Gene action	Phenotype	Reference
Adc	Arginine decarboxylase (Polyamine synthesis)	Drought resistance	Capell et al., 2004
codA	Choline oxidase (glycinebetaine synthesis)	Recovery from a week long stress	Mohanty et al., 2003
COX	Choline oxidase (glycinebetaine synthesis)	Stress tolerance	Su et al., 2006
HVA1	Group 3LEA protein (late embryogenesis abundant)	Dehydration avoidance and cell membrane stability	Babu et al., 2004
OCPI1	Chymotrypsin inhibitor like 1 (proteinase inhibitor gene)	Stress tolerance	Huang et al., 2007
OsLE A3-1	LEA protein (late embryogenesis abundant)	Drought resistance for yield in the field	Xiao et al., 2007
P5CS	Pyrroline carboxylate synthase (proline synthesis)	Reduced oxidative stress under osmotic stress	Hong et al., 2000
P5CS	Pyrroline carboxylate synthase (proline synthesis)	Increased biomass production under drought stress	Zhu et al., 1998
RWC3	Aquaporin (water channel protein)	Stress response	Huang et al., 2007
TPS	Trehalose-6-phosphate synthase (Trehalose synthesis)	Drought tolerance	Jang et al., 2003
TP	Trehalose-6-phosphatase (Trehalose synthesis)	Drought tolerance	Lee et al., 2003

Table 2. Achievements made in overexpression of candidate genes through transgenic approach in rice

3.3 Proteomics

In general, abiotic stresses cause considerable dysfunction in proteins, proteomic approaches focused on protein changes in response to stresses and explore the functional network of protein. A global protein expression profile can be investigated using two dimensional polyacrylamide gel electrophoresis (2DE) technique coupled with protein

identification by mass spectrometry (MS). This technique facilitated identification of new proteins of interest and elucidated the expression profile, post translational modification, interactions and *de novo* synthesis of proteins (Peck, 2005). Salekdeh et al., (2002) investigated the drought responsiveness using lowland indica (IR62266) and upland japonica (CT9993). They quantify nearly 1000 rice leaf proteins out of which 42 responded to stress. Similar such studies have identified several proteins based on its function and classified them into two groups. One group of proteins such as heat shock proteins (HSPs), late embryogenesis abundant protein (LEA), Dehydrin proteins, RuBisCo and reactive oxygen species (ROS) play a direct role in protecting the plant cells against stress by involving in osmotic adjustment, chaperon like activity and scavenging of reactive oxygen species. The second group of proteins are viz., mitogen activated protein kinase-MAPK and calcium-dependent protein kinases-CDPK (Ludwig et al., 2004), salt overlay sensitive-SOS kinases (Zhu, 2001), phospholipases (Frank et al., 2000) and transcriptional factors (Choi et al., 2000) are actively involved in signaling cascades and transcriptional control. Overexpression of signaling factors known to control a broad range of downstream events and has resulted in superior tolerance (Umezawa et al., 2006)

Huge amount of data generated from proteomic studies provided useful information on individual enzymes and transporters that are involved in stress responsive network including protein modifications, interactions and *de novo* synthesis. Further the information would be helpful in developing biomarker for molecular cloning. However, the application of a proteomic approach at the whole cell level is limited by several factors such as protein abundance, size, hydrophobicity and other electrophoretic properties (Parker et al., 2006; Timperio et al., 2008). Moreover, low abundance proteins including regulatory proteins and rare membrane proteins are out of scope of most proteomic techniques, it is due to chemical heterogeneity of proteins associated with diverse functions within a cell. The limitation could be resolved using comprehensive protein extraction protocol for proteome analysis.

4. Conclusion and future prospects

The present review summarizes the achievements of breeding enhanced tolerance towards water deficit condition in rice. In early 1980's large number of studies on drought stress have identified some morphological features such as strong root system, short stature plants, reduced leaf area and limited tillering ability were capable of maintaining high plant water status to enhance drought avoidance. Among those features, the most important is the root system as it ensures extraction of soil water from greater depth in upland regions and maintains high LWP during stress. While, in rainfed lowland regions, soil forms hard encrustation and inhibit root penetration when the available soil moisture is exhausted. The genotypes with dense and thick roots were suggested to improve selection efficiency. Further, physiological studies in the past have provided knowledge on complex network of drought stress related traits and suggested relevant drought related determinants such as WUE, osmotic potential, utilization of stem reserve, dry matter production, etc., that could be used to achieve high potential (Blum, 2005).

Conventional breeding program effectively utilized those traits and achieved drought tolerance by generating reasonable number of cultivars. However, the program is limited by lack of appropriate screening technique. It is because drought stress can occur at any time of the developmental stage; starting from sowing to grain maturity. Generally it is widely

accepted that stress at reproductive phase is critical and deserves attention. However, genotypic response that contributes to drought stress avoidance/ tolerance is largely depends on the genetic mechanism of tolerance in the target environment (Fukai and cooper, 1995).

With the advancement in biotechnological tool, the genetic basis of drought tolerance has received considerable attention. Gene governing quantitative traits were identified using a variety of molecular markers and their loci controlling drought tolerance were mapped on the chromosomal regions. Mapping of QTL has resulted in greater understanding of genetic phenomenon of drought tolerance traits. Despite the significant progress in cereal genomics, the QTL approach has not widely practiced in marker assisted breeding and still remains a major challenge. The efficiency of MAS is hampered by the complexity of gene governing grain yield, epistatic interactions and epigenetic variation among QTLs. However, Tuberosa and Salvi (2006) opinioned that conscious selection of mapping population and careful introgression of specific alleles from genotype to other, through pyramiding could bring success to MAS.

In the last decade, transgenic and functional genomic approaches offered a reliable promise in identifying stress responsive genes, pathways and deciphering the mechanism of stress tolerance. Further it enabled to solve several essential key questions associated with stress tolerance through gene expression profiling and engineering of tolerant traits. A large number of functionally characterized genes, transcriptional factors and promoters were introduced by such methods to enhance tolerance against abiotic stresses. Although several reports have highlighted the significance of this approach (Cattivelli, et al., 2008; Kamoshita et al., 2008; Umezawa et al., 2006; Vij and Tyagi, 2007; Yang et al., 2010), introgression of genomic portion often associated with undesirable agronomic traits and only very few field screening and genetic transformations have resulted in improved grain yield under drought condition. It is likely due to the fact that interaction between number of edaphic and climatic factors poses difficulty in screening of stress tolerance (Ashraf et al., 2008). Further it is anticipated that transcriptional regulation as well as post transcriptional gene plays a major role in determining the tolerance against various stress. Therefore while using functional genomics, it is important to consider the phenomenon of regulatory network including siRNA and miRNA to fine tune the expression of genes associated with stress responses (Yang et al., 2010). Indeed, the post genomic era has offered a great potential to increase the efficiency of breeding by determining the phenotype more precisely. Further, the challenge in stabilizing high yield under drought condition could be achieved in near future by integrating plant breeding with multidisciplinary approach based on plant physiology, functional genomics and by adapting comprehensive screening technique.

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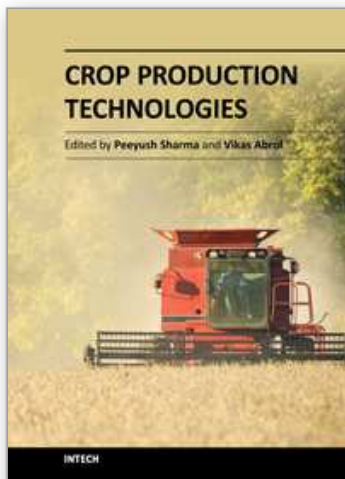
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Crop production depends on the successful implementation of the soil, water, and nutrient management technologies. Food production by the year 2020 needs to be increased by 50 percent more than the present levels to satisfy the needs of around 8 billion people. Much of the increase would have to come from intensification of agricultural production. Importance of wise usage of water, nutrient management, and tillage in the agricultural sector for sustaining agricultural growth and slowing down environmental degradation calls for urgent attention of researchers, planners, and policy makers. Crop models enable researchers to promptly speculate on the long-term consequences of changes in agricultural practices. In addition, cropping systems, under different conditions, are making it possible to identify the adaptations required to respond to changes. This book adopts an interdisciplinary approach and contributes to this new vision. Leading authors analyze topics related to crop production technologies. The efforts have been made to keep the language as simple as possible, keeping in mind the readers of different language origins. The emphasis has been on general descriptions and principles of each topic, technical details, original research work, and modeling aspects. However, the comprehensive journal references in each area should enable the reader to pursue further studies of special interest. The subject has been presented through fifteen chapters to clearly specify different topics for convenience of the readers.

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